ECOLOGY OF TILIA AMERICANA

I. COMPARATIVE STUDIES OF THE FOLIAR TRANSPIRING POWER

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 253

JAMES E. CRIBBS

(WITH THIRTEEN FIGURES)

Introduction

Up to the present time transpiration studies have been conducted almost exclusively with potted plants, or upon plants which were growing under controlled conditions. This is due to the fact that most of the investigation has been purely physiological in its aims; and since the factors influencing this process are numerous, they can evidently be more definitely calculated in controlled habitats than in natural ones.

It has been the investigator's aim to carry this line of experimentation into the field, in an endeavor to determine what differences occur in the relative foliar transpiring power of a certain species when growing in different environments. It was at once recognized that the complication of factors which influence transpiration is considerably increased, and the precision with which they may be measured and the relative values to be attributed to each are perhaps less exact than when such investigation is made under greenhouse or laboratory conditions. Nevertheless, there are certain problems which of necessity must be worked out under field conditions, especially when we wish to determine the ecological value or relationship of the environment.

For this investigation *Tilia americana* was chosen because it, perhaps more than any other of our tree species, grows under a wide range of environmental conditions. This is especially true when we consider its unusual ability (as a member of a mesophytic forest) to surmount moving dunes which chance to advance upon it. This ability of *Tilia* to persist on the moving sands brings it into a set of varying conditions which are widely different from those of its normal mesophytic environment, and affords an excellent opportunity to investigate certain ecological and physiological features which are brought under particular stress because of the abrupt change in growth conditions.

Five stations for investigation were selected on the dunes near Miller, Indiana, and will be designated here as *A*, *B*, *C*, *D*, and *E*.

FIG. 1.—Station *A*, showing *Tilia* on forested complex, associated with *Psedera*, *Smilacina*, *Acer*, and *Prunus*.

Studies were conducted also at station *F* in a mesophytic forest on morainic clays in western Pennsylvania, that a comparison might be had for different soil conditions.

Station *A* (fig. 1) is located on an established dune complex which has advanced to a state of mesophytism in regard to both the tree and herbaceous vegetation. It is well sheltered from the strong lake winds, and is not exposed to the intense light and the accompanying high temperatures of the open sand areas.

Station *A* lies deeper in the complex than *B* (fig. 2), which is situated at the base of a forested dune and is not more than 15 m.

from the edge of a blowout. The conditions are very similar at *A* and *B* so far as the humus is concerned. This has attained a thickness of approximately 5 cm., which is indicative of a relatively long period of stability. The presence of a well defined humus is correlated with a very rich development of herbaceous undergrowth and tree seedlings.

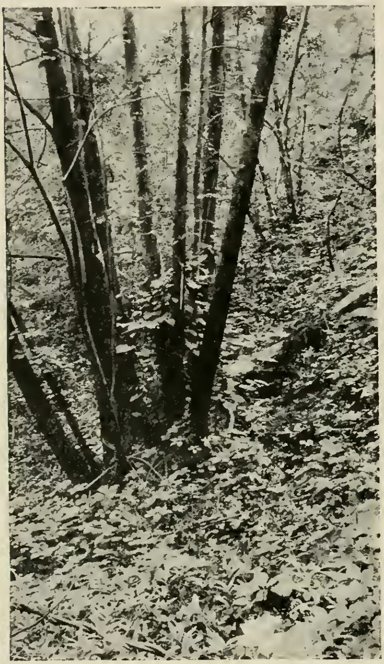

FIG. 2

FIG. 3

FIGS. 2, 3.—Fig. 2, station *B*, showing position of *Tilia* at base of well established dune and with same plant associates; fig. 3, station *C*, where *Tilia* is located on edge of blowout; humus being broken up by sand movement, and access of wind and light much greater than at *A* or *B*.

Station *C* (fig. 3) is located on a west-facing slope on the edge of a blowout where there is a ready access to strong winds. The exposure to light is much greater here than at either *A* or *B*, especially in the afternoon when the sun's rays fall vertically upon the slope, while the stations in the forested complex are deeply shaded. The free sand movement has destroyed the humus and with it a large part of the accompanying herbaceous vegetation, thus developing a situation of greater openness and more intense exposure.

Station *D* (fig. 4) is located on the lee slope of an advancing dune. In most respects this position is more xerophytic than that at *C*, for there is a complete absence of humus and herbaceous

FIG. 4

FIG. 5

FIGS. 4, 5.—Fig. 4, station *D*, with *Tilia* on lee slope of advancing dune; sand advance rapid at this point, and absence of humus further inhibits herbaceous development; plant associates: *Cornus stolonifera*, *Ammophila arenaria*, and *Prunus virginiana;* fig. 5, station *E*, showing *Tilia* located on crest of high dune and exposed to most desiccating conditions found in dune environments.

undergrowth. The incipient rays are strongly reflected from the open sand, giving a very high light intensity and considerable increase in temperature. Being on a south-facing slope, the greatest exposure occurs in the late forenoon, followed early in the afternoon by shade which is continuous until evening.

Station *E* (fig. 5) represents the most exposed habitat to be found on the open sands, as it is situated about 25 m. above the lake on the crest of an eroding dune which is exposed to wind from all points of the compass. The water content is less at this point than at lower levels and the light intensity becomes the greatest, the sun striking the station about 8:00 A.M., from which time it remains directly exposed until evening. The absence of humus and the exposure to wind combine to give a high sand mobility, which means a most unstable kind of habitat.

FIG. 6.—Station *F*, showing *Tilia* in mesophytic forest on clay soil; chief plant associates: *Osmorhiza*, *Adiantum*, *Caulophyllum*, *Aralia*, and *Actaea*.

Station *F* (fig. 6) is located in a forest, the chief tree members of which are *Acer*, *Liriodendron*, *Castanea*, and *Prunus serotina*. The herbaceous undergrowth includes such mesophytic species as *Aralia racemosa*, *Adiantum pedatum*, *Osmorhiza longistylis*, *Viola pubescens*, etc. The humus at this station has a depth of about 5 cm. and the underlying soil is a mixed morainic drift.

Methods

The cobalt chloride paper method was employed to determine the relative transpiring power. This method, first used by STAHL (15), has been improved and employed by subsequent investigators and is undoubtedly the one in present use which is best adapted for work in the field. Whatman's filter paper no. 30 was used throughout this work and was treated with a 3 per cent solution of cobalt chloride and prepared in accordance with the method described by LIVINGSTON and SHREVE (10). Preliminary tests were made with the plain paper and the tricolor slips of LIVINGSTON and SHREVE, and as essentially the same coefficients were obtained the tricolor paper was discarded as being more difficult to prepare and less easily handled in the field. The plain paper has the additional advantage of being somewhat slower, and is thus more satisfactory when used at stations on the open sands, for the change in color was found to take place so quickly that even the paper with longer time values was frequently difficult to read. The probability of error arising from short time periods was largely eliminated by increasing the number of readings from the usual 5 to about 8 or 10, and the time recorded in each instance was the average of all readings made.

The paper was applied to the leaf surface by means of the clip devised and described by LIVINGSTON (8). At each of the stations leaves were chosen which were about 1 m. above the ground; readings were taken from the same relative position on the different leaves; and so far as possible the same set of leaves was employed in each subsequent day's work. Records were taken from 2 leaves at each station, usually at hourly intervals, beginning as soon as there was sufficient light to observe the color change and continuing until darkness prevented further reading. Records given here were taken from the abaxial (stomatal) side only.

The indirect method of determining the color change over the standard evaporating surface, as suggested by BAKKE (1), was used during the second summer's work, thus making it unnecessary to take the standard cup of LIVINGSTON and SHREVE into the field.

Various devices were tried for heating the hygrometric paper to force off the water of crystallization, for considerable difficulty was experienced because of the prevalence of stong lake winds, so a special lamp was devised and used for this purpose. The chief difficulty with the acetylene lamp was to get a steady flame for a long period of time. That which was finally employed consisted of a railroad lamp, with a round wick, which had an oil capacity of about 0.5 liter. A tubular piece of tin was fashioned so that it had a transverse dimension of about 8 cm. and a length of 23 cm. This was fitted to the base by means of 3 guides so as to leave a space of about 2 mm. below for ventilation. Into the upper end was set a small tin cup such as may be obtained at any hardware store, and over this a screen lid was placed for use when working in a high wind. For ventilation above the flame, a ring of small holes was cut about 2.5 cm. below the level of the inserted cup. This lamp was found to be readily controlled, burns alcohol or kerosene equally well, can be used successfully in a strong wind, and burns continuously for 48 hours or more without refilling or adjustment.

Relative humidity was calculated hourly by means of the sling psychrometer, such as is in use by the United States Weather Bureau, and the wet bulb depression was referred to a standard table as given by MARVIN (12) to obtain the relative humidity values.

Soil temperatures were recorded for depths of 2 dm. and 4 dm. by means of a centigrade thermometer mounted on a cylindrical piece of hickory which was well adapted for inserting into the sand. Atmospheric temperature records were taken and recorded hourly during each day of experimentation.

Soil samples were collected at the different stations on the days when these were worked and the moisture computed on the basis of dry weight. From these results growth water was calculated by the equation $GW = SW - WC$, in which SW = total soil water and WC = the wilting coefficient. Samples were taken from depths of 2 and 3 dm. and dried for 6 days at a temperature of 100° C.

The wilting coefficient of the soil was computed by the centrifuge method of BRIGGS and MCLANE (4). The moisture equivalent was obtained directly and the wilting coefficient derived from this by the equation of BRIGGS and SHANTZ (3), $\frac{ME}{1.78} = WC$.

The evaporating power of the air was recorded by means of the porous clay cup of LIVINGSTON (7). Hourly readings were readily secured by mounting the atmometer on a graduated burette tube which was refilled when the water column fell to a point about 25 cm. below the level of the cup.

Field work was conducted under diverse weather conditions to discover to what extent the varying of such factors as relative humidity, wind, light, temperature, etc., might influence the rate of transpiration in the field, and to compare its relative influence in the different environments. In each instance readings were taken at stations *A*, *B*, and *C* on the same day. The same may be said for stations *D* and *E*. Fig. 7 represents the records of relative transpiring power, temperature, relative humidity, and evaporation for *A*, *B*, and *C* on July 21, 1918. As in the following graphs, the scale to the left is for the index of foliar transpiring

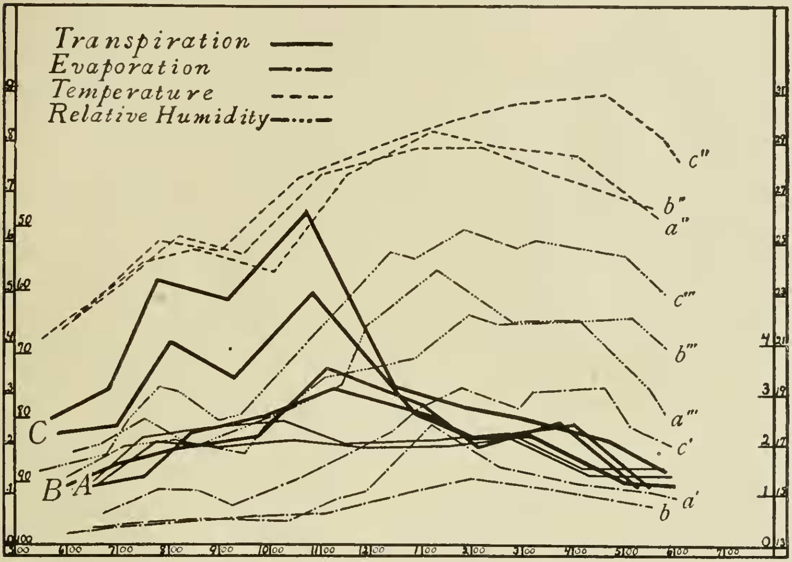

FIG. 7.—Graph giving transpiration, temperature, evaporation, and relative humidity curves of stations *A*, *B*, and *C* for July 21, 1918; scale similar in all following graphs (see text).

power; the inner one to the left is for relative humidity; the inner one to the right is for evaporating power of the air and is expressed in cubic centimeters per hour; and the scale to the right records the atmospheric temperature in degrees centigrade. Time is indicated at the bottom of each graph.

It will be noted that there is a close parallelism between the curves representing temperature, evaporation, and relative humidity. This is in fact what would be expected, as these factors are closely interrelated. Accompanying the opening of the stomata in the morning, there is a rise in the transpiration indices, and their curves follow closely those of the factors just mentioned until about 11:00 A.M., when a marked divergence occurs. The transpiration curve declines rapidly from a maximum at this time, while the curves representing relative humidity, temperature, and evaporation continue to rise until about 2:00 P.M., following which there is a gradual decline. This feature is little in evidence in the graph of station *A*, but becomes more so in those of *B* and *C;* that is, the divergence becomes more and more conspicuous with an increase in exposure of habitat. This same feature will be found to recur with greater prominence when we consider the data of stations *D* and *E* on the open sand.

There has been considerable discussion concerning the interpretation of this sudden decline: LLOYD (11), following his investigation of stomatal action in *Fouquieria* and *Verbena*, concluded that the earlier view that stomatal movement controlled the transpiration rate was not entirely true, for there may be an increase in the transpirational loss for some time after the maximum opening; and there was found to be frequent decrease and subsequent increase in the afternoon, with little or no accompanying stomatal movement. RENNER (13) advanced the concept of "saturation deficit" to explain this behavior in transpiration, and LIVINGSTON and BROWN (9) in the following year discussed this behavior under the "incipient drying" theory. These are essentially the same concept, namely, that following the rise in the transpiration rate which accompanies the stomatal opening in the morning a point may be reached when the turgidity of the mesophyll cells of the leaf becomes sufficiently reduced to increase the surface tension of the water films in the walls. A check in the molecular diffusion of water from the cells follows. The increased concentration of the cell contents would then exert additional pull on the water in the translocating system, and a restoration of turgor may then follow without visible wilting occurring in the leaf. The length of time elapsing before the restoration of turgor depends largely upon the evaporating power and temperature of the atmosphere, also upon the relative humidity of the air, and in some cases upon growth water. In recording the daily transpiration march in *Tilia* this saturation deficit was found to be very characteristic, especially at times when the relative humidity is low. It is also induced more readily when the growth water is near the zero point.

There is another condition, however, under which a very similar behavior in the graph is noted and may very easily be confused with the preceding. This would be especially liable to happen when one is employing the porometer and cobalt chloride paper only, as was done in the work of TRELEASE and LIVINGSTON (16). This cause lies in a sudden change in relative humidity. Thus if there is a sudden increase in relative humidity the effect on the transpiration index is to depress it. Such depressions may be detected from saturation deficits by an accompanying lowering in the curve of evaporation, for when it is due to a deficit the evaporation curve will be high. Inasmuch as a depression in transpiration caused by an increase in relative humidity is not accompanied by a closure of stomata, according to LLOYD (11), the porometer of course would continue to record the relative stomatal opening, and a divergence in the graphs would result. Instances of this appeared a number of times during the experiments, and were very marked on the occurrence of transient showers.

The sudden depression at 8:00 A.M. in graphs of station *C* (fig. 7) is due to this influence. It will be noticed that there is a corresponding increase in relative humidity, with a lowering of temperature and evaporation power. The behavior at this time is definitely attributed to the passing of a thundershower some distance to the south. It is interesting to note that the influence is more pronounced at station *C* than at *A* or *B*, especially as regards transpiration and evaporation. The drop in evaporation at *C* is attributed mostly to a sudden period of calm which had less effect at *A* and *B* because of their more sheltered position. The greater effect in the relative transpiration curve at *C* is probably to be interpreted as the result of a greater susceptibility of the leaf to a change in relative humidity when transpiring at a high rate.

The curves in fig. 8 were plotted from readings taken at station *D* on September 2. One of the outstanding features of this graph is the parallelism in all the curves. It will be observed that the maxima of transpiration coincide with those of temperature, evaporation, and relative humidity; and that there is an absence, or at least almost a complete absence, of an afternoon saturation deficit. In both of these respects this graph differs from the preceding one. The difference was found to be related to the atmospheric conditions. The evaporating power of the air

FIG. 8.—Graph plotted from data taken at station *D* on September 2, 1918; parallelism of curves and absence of saturation deficit due to high relative humidity.

was low throughout the day, never reaching 1 cc. per hour, while ordinarily at station *B* it became 2 cc. or more per hour by 2:00 P.M.; the temperature was low and the humidity high. This combination of factors in the field was always found to favor parallelism of curves and an absence of a saturation deficit. Under such conditions the maxima usually occur later in the day than when the deficit is developed.

At 7:30 A.M. there occurs a sudden fall in the transpiration indices which resembles the deficit drop. This was due to a sudden shower which began at 7:40 and lasted until 8:20. If the stomatal behavior is similar in *Tilia* to that found by LLOYD (11) to exist in *Fouquieria*, *Verbena*, and *Ampelopsis*, a porometer curve, if such had been made, would probably have continued to rise from 8:00 to 10:00 A.M. and would have given the type of curve that is obtained when a true deficit occurs. The evaporation curve alone shows that this was not a deficit depression, and one could safely infer the same from the much higher maximum that immediately follows; but if such a drop had occurred near midday, the second higher mode may not have occurred and a fall identical with that of the saturation deficit may have resulted. It will be noted that, notwithstanding the low evaporation rate, the transpiration index is quite high. This was found to be true for positions on the open sand, although under the same atmospheric conditions on humus the index was always much lower. This is probably largely due to the greater light intensity in the former position, and to a certain degree to higher temperatures.

It may be interesting to note the following atmospheric conditions in their general relation to the transpiration indices for this particular day: 5:00–7:20 A.M., partly cloudy; 7:20–7:40, cloudy; 7:40–8:20, rain; 8:20–9:30, cloudy; 9:30–10:00, clearing; 10:00–12:30 P.M., sun; 12:30–3:00 P.M., cloudy; 3:00–6:00 P.M., clear, but station shaded. From these data it will be seen that the drop from 1:00 to 3:00 P.M. was probably due to the sudden cloudiness of that period, which may have caused sufficient closing of the stomata to effect a depression. There is also a small drop in temperature and relative humidity at this time which would also have their influence, although not recorded by the atmometer. It should be said, however, that the white cup is less influenced by light changes than is the leaf (LIVINGSTON 6), and this was found to be most noticeable on the open sand when the index of transpiration was high.

One of the most striking relations that appeared in these comparative studies was found in the readings taken at the stations located on humus and those on the open sand during the latter part of the summer. As previously stated, stations *A* and *B* are in a forested complex which has a well developed humus and an abundant herbaceous undergrowth, and *C* is on the edge of the same complex, where it is being destroyed by a blowout. These stations, when compared with *D* and *E*, stand out in contrast by their greater mesophytism. This is true in regard to the texture of their foliage and its richness; but during the months of August and September the *Tilia* complex rapidly undergoes a change which is very noticeable in the vegetation and is conspicuous in the relative transpiration indices. This change is initiated by an early reduction of the soil moisture to the wilting coefficient, evidently because of the heavy vegetation the sands are supporting and the excessive transpiration rates caused during this period by the highly desiccating atmospheric conditions. Stations *D* and *E* show, during this same period, a higher growth water content on the exposed dunes; and the abscission which is carried on rapidly in the *Tilia* complex is entirely unnoticed here until much later. The greater soil moisture on the open sand as compared with the pine and oak dune stages has been pointed out in the work of FULLER (5), and is seen to be similar for the *Tilia* complex. Fig. 9 emphasizes this relationship. The data for stations *A*, *B*, and *C* were taken on August 26, and that for station *E* on August 11. Although the 2 sets of readings were not taken at the same time, the atmospheric conditions on the 2 days were practically identical. Both days were sunny throughout, and the general parallelism of temperature, evaporation, and relative humidity was rather unusual. Curves for these factors were plotted for stations *A* and *E* only.

The transpiration indices of *A*, *B*, and *C* were all very low, that of *C* being slightly higher than *A* or *B*. They rose slowly in the morning from a low point and reached a low maximum at 8:00–8:30 A.M. A deficit occurred then because the soil moisture had reached the wilting coefficient, and the indices remained low throughout the day, rising slowly in the evening as the leaves regained their turgor. Visible wilting occurred about 10:30 A.M. at these stations, and was sufficient to cause stomatal closure. The temperature, evaporation, and relative humidity are seen to have remained high, reaching a maximum about 3:00 P.M., after which they declined rapidly.

A very different behavior occurred at station *E*, where the exposure is more intense. The growth water here was found to be 0.679 per cent at 2 dm. and 1.054 per cent at 3 dm., but the leaves remained turgid throughout the day, and there was no visible wilting. The transpiration index at 6:00 A.M. was quite high, and rose rapidly during the morning to a maximum at 12:00 noon. Here a saturation deficit was developed and a sudden

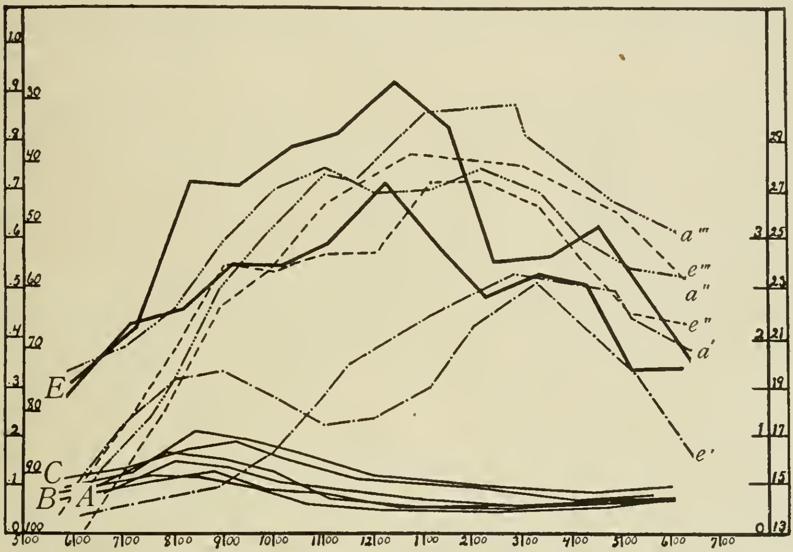

FIG. 9.—Graphs for stations *A*, *B*, and *C* on August 26 and station *E* on August 11, 1918; high transpiration index occurs on open sand with afternoon saturation deficit, while indices for humus stations remain low, due to visible wilting.

depression occurred until about 3:00 P.M., which was followed by a second low mode at 4:30.

This curve is a very typical one for a clear day at this position, in that there is a rapid rise in the morning to a high maximum, and a following clearly marked depression due to a saturation deficit, but no visible wilting occurs; then a second low mode in the afternoon about 4:00 P.M., followed by a rapid decline with the closing of the stomata in the evening. The morning maximum occurs from 9:00 to 12:00, unless disturbed in some way by such influences as thundershowers and sudden shifting of wind to or from the lake with accompanying atmospheric changes in temperature, relative humidity, etc.

The usual pronounced saturation deficit that occurs on the exposed sands is shown in fig. 10, which is a graph of readings taken at station *E* on July 27. There was a very rapid rise to a maximum at 9:30 A.M., at which time the water loss presumably

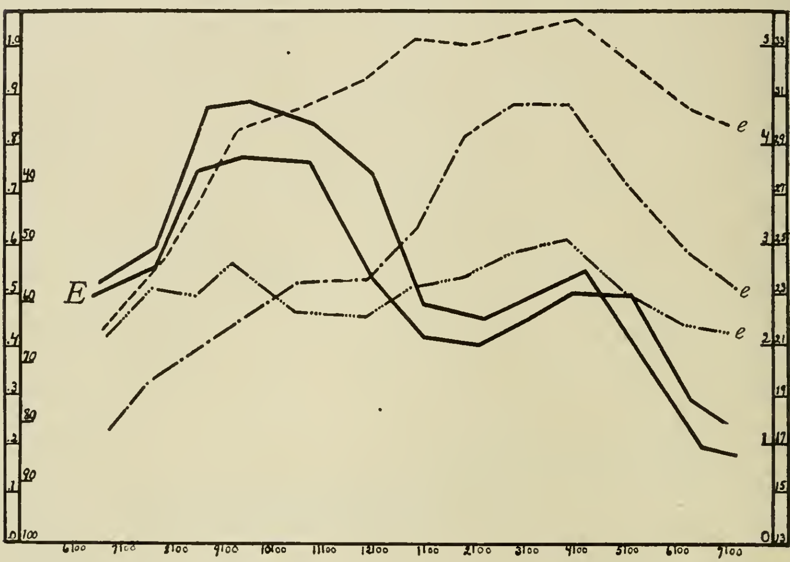

FIG. 10.—Graph plotted for station *E* on July 27, showing typical saturation deficit developed in open dune environments on clear days with temperature high or relative humidity low.

equaled the maximum translocating ability of the plant under the conditions. Then as a deficiency was created in the cells by an excessive loss, a drop in the index occurred until the turgor was regained. A second low mode occurred at 4:00 P.M., a feature recurring in all records taken at stations *D* and *E*, in which an appreciable deficit was developed. Although the decline in the relative transpiration index was considerable in the early afternoon, there was no visible wilting.

Fig. 11 is a composite graph in which the curve for each station is plotted from the average of all the readings taken. This figure shows the relative transpiring power of *Tilia* in the different dune environments, and it will be seen that there is a very pronounced increase in the index of transpiration when considering the stations in their order from the mesophytic to the more xerophytic habitats.

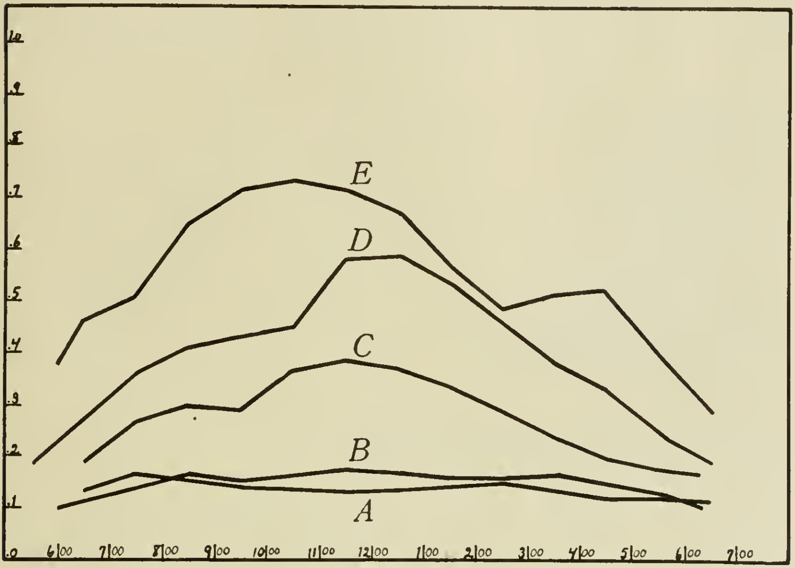

FIG. 11.—Composite graph of all transpiration readings taken at stations *A*, *B*, *C*, *D*, and *E*, showing increase in transpiring power accompanying increased exposure of habitat.

These curves being averages, and hence not recording daily variations, do not give to best advantage the typical daily curve. The occurrence of the maximum about 12:00 noon in the more mesophytic situations, however, and an earlier occurrence from 9:00 to 11:00 A.M. on the open sands, is noticeable even in the average graphs, as is also the earlier morning rise characteristic of the exposed stations.

Fig. 12 includes averages of all the different factors taken in connection with the dune transpiration studies. The unit spaces at the top of the graph have the following values: evaporation

5 cc. per unit; transpiration 0.1; relative humidity 15 per cent; soil temperature 7° C.; atmospheric temperature 10 per cent; and growth water 1 per cent per unit. From these it will be seen that the conditions existing at stations *A* and *B* are closely similar; but from *B* to *E* the stations represent a graded series of habitats as regards these factors, just as clearly as they do when we consider their comparative positions in the vegetative cycle. This graded variation found in the dune environments is much more pronounced than that for different situations on clays, which will

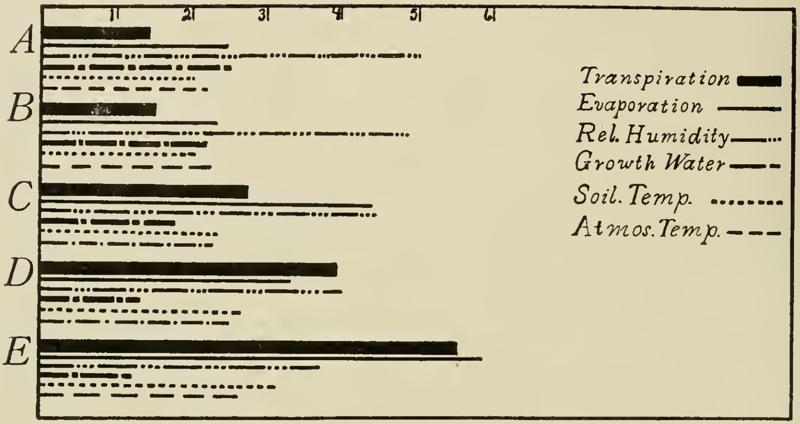

FIG. 12.—Comparative graph illustrating conditions of transpiration, etc., for the 5 dune environments; close gradation of factors evident here; increase in transpiration accompanying decrease in growth water is characteristic of dune habitats.

be mentioned only briefly in this paper. The increase in relative transpiring power that occurs with an increase in exposure of habitat is very evident.

Concerning evaporation, the only variation occurs at station *C*. Here the water loss is considerably more than at *D*. This is because of the greater access of wind at *C*, which is located on the edge of a blowout, while *D* is on a protected lee slope where only south and southeast winds have access.

The average relative humidity decreases rapidly from *A* to *E*, and is almost parallel with the increase in the transpiration index. Variation in humidity has been considered the most potential single factor influencing the transpiration index (Briggs and Shantz 2), and so far as considered in these studies it has been found to be a factor of the first order. It is not always the controlling one, however, for there are frequent variations in the daily march which owe their appearance to other causes. Temperature, stomatal movement, and growth water, for instance, at any given time may become the dominating factor, only to be succeeded as the conditions vary by some other which for the time being replaces it.

The proportional increase in the soil temperature over that of atmospheric temperature from *A* to *E* is of interest, and it may safely be inferred that high soil temperatures have a prominent part in the maintenance of the water supply, and hence indirectly concern the transpiration rate. Until more accurate quantitative measurements are made upon the effect of increase of temperature of the soil upon the water absorbing power of roots, however, the quantitative influence of this factor can only be speculated. Such work as has been done by Rysselberghe (14) on the effect of temperature changes on the rate of osmotic transfusion through semipermeable membranes leads to the conclusion that the much higher soil temperature, as of *E* over station *A*, must be one of the factors which enable the exposed plants to take over water from the soil with sufficient rapidity to withstand the much higher transpiration loss.

One of the noteworthy features of the dune studies appears in the relation of the growth water to transpiring power. It may be seen from the figure that there is a low average of growth water at all stations, that for *A* being only about 2.46 per cent and that for *E* 1.25 per cent. While it is true that the highest average is at *A*, the greater percentage here is due to the higher content during the earlier summer months. During the latter part of July and August, however, the water available for plant absorption decreases more rapidly than on the open sand, and the frequent drop in soil moisture to the wilting coefficient produces a period of stress and leads to early abscission. Meanwhile the growth water on the moving complex remains practically constant, especially at a depth of 3 dm. or below, where it is about

1.25 per cent or more. This greater constancy is attributed to the moving mulch of dry sand which breaks the continuity of surface films in the soil particles, thus preventing rapid evaporation. This ability of a plant to maintain a higher transpiration index with a growth water content of 1.25 per cent than the same species does with 20 per cent or higher, such as is commonly true for clays, indicates that the amount of growth water has but little relation to the transpiration index so long as the soil moisture content remains above the wilting coefficient. This gives a somewhat unusual aspect to the question of mesophytism and the part played by soil water as a factor in plant growth. So far as *Tilia* is concerned, it produces more vigorous vegetative structures, which retain their activities later in the summer, when growing in open situations on sand than when in the forested dune complex; and the factor of greatest importance seems to be, not the average growth water of the soil, but whether the available moisture repeatedly falls below the wilting coefficient. So long as it is above that point, although it is by only a very small percentage, the normal activities, including high transpiration, are carried on.

There is one point concerning this relation which needs investigation, however, namely, the relative extensiveness of the root systems in the two situations. I am inclined to the idea that the ability of *Tilia* to develop adventitious roots when covered by an advancing dune may enable such individuals to draw their water supply through a root system the absorptive surface of which is greater in proportion to the amount of foliage than is true of this species when growing in the forest complex. Another point of probable difference is that the individuals on the open sand may obtain a considerable portion of their water from a greater depth than do those on the humus; but the extent to which the root systems persist when submerged by advancing dunes has never been worked out.

As indicated by the averages shown in fig. 11, the situation at *E* is distinctly more xerophytic than at *A*. Every fact recorded in the experimentation points to this conclusion. The size, general shape, and texture of the leaves at station *E* are also distinctly xerophytic, but it has been noted that notwithstanding this the transpiration index is higher, a fact not at all in accordance with the behavior of desert plants so far reported, for they are characterized by a low transpiration index, as pointed out by several workers. With this fact in view BAKKE (1) has suggested the foliar index of relative transpiring power as a test for the mesophytism of a plant, as follows: "As a result of the preliminary study, it may be suggested that plants exhibiting a diurnal foliar transpiring power of less than 0.30 may be regarded as xerophytes, while those exhibiting indices above 0.70 may be considered mesophytes." It may be seen at once that the behavior in *Tilia* is the reverse of that common to desert plants, and hence an application of this test would lead to confusion. I believe with BAKKE, however, that with certain reserve this method may be used as a fair indicator of mesophytism, provided two precautionary measures are taken: first, that the species under consideration be chosen in its normal environment and not in an abnormal or forced one; and second, that hourly readings be taken for at least two full days and that the relative humidity and temperature conditions be carefully employed in calculating the results. This latter precaution is necessary because of the great variation in the index at different times of the day, in the first place, and because of the wide variation of the indices at any particular hour on two successive days when the relative humidity or temperature has undergone considerable change.

The development of a xerophytic leaf under unusual conditions of exposure has been found in *Tilia* to result in a leaf less effective in preventing water loss than are desert types. This may be attributed to a lagging of the effect behind the causal factors. On the other hand, such lagging may be considered as not occurring, for there is always a favorable balance in water relations which permits a greater vegetative activity than would be possible in desert plants, and becomes possible on the open sands only because of a sufficient and permanent growth water throughout the growing season.

At station *F* there is considerable difference in the environment, and the factors accompanying it, from that of the dune series. It has already been noted from the introductory description that the undergrowth is composed of a more shade-requiring assemblage than even the most mesophytic positions found on the established dune complex. The humus is slightly more developed, but the soil underlying it is very different, and unlike in the forested dune habitats the growth water was always adequate to support an abundant and diversified vegetation, and never reached the wilting coefficient. The average available water at 2 dm. was 19.40 per cent and the minimum 12.45 per cent. Thus if growth water is inducive of a high transpiration, one would expect to find it here, but the average transpiration at this station for 5 complete days' readings was only 0.16, an index practically identical with that of station *A* of the *Tilia* forested complex where the growth water averaged 2.5 per cent.

The same tendency displayed by the dune graphs to show curves with a single mode recurs here where the mesophytism is greater. The maximum power of transpiration comes later in the day, commonly from 12:00 to 2:00 P.M., and is more frequently coincident with the maxima of temperature, evaporation, and relative humidity. This relation is shown in fig. 13, which is a graph of station *F* on June 14. At this time there was a growth water content of 26.74 per cent and a relatively low humidity. The temperature was low, while the evaporation was high when compared with the transpiration, higher than commonly found in dune environments. The morning rise of the transpiration index was very slow and the maximum reached was not very high. On this particular day it was clear until about 2:00 P.M. with increasing cloudiness through the afternoon, followed by showers at 8:00 P.M. Although it was clear during the forenoon the station was shaded throughout the period.

The fact that direct sun upon the leaves in a habitat of this sort almost always leads to a rapid increase in the transpiration rate would suggest that the low light intensity of the densely shaded forest is one of the chief factors leading to the low average commonly found there.

Summary

1. Cobalt chloride standardized paper was found well suited for comparative studies in the relative transpiring power of leaves in the field.

2. The daily march of transpiration in *Tilia* was found to vary greatly for the same leaf on different days. This variation was found to be influenced by relative humidity, temperature, light intensity, soil moisture, and presumably by soil temperature.

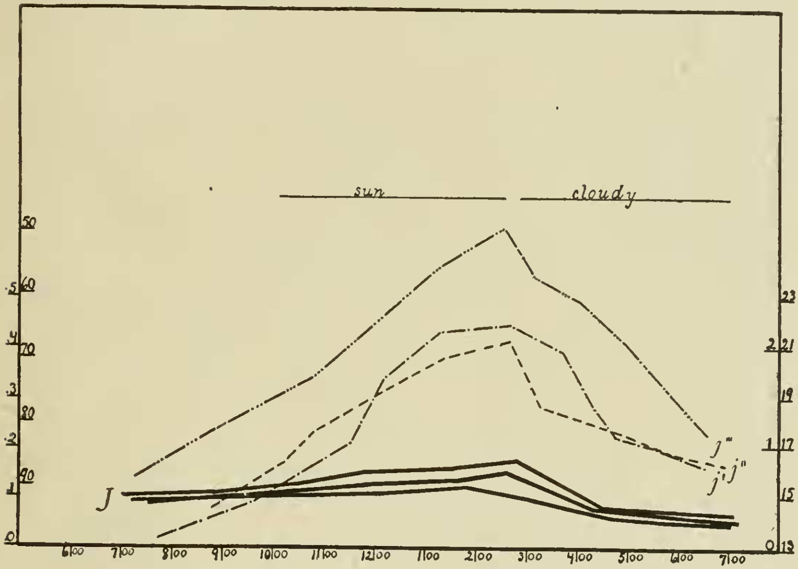

Fig. 13.—Typical graph illustrating low transpiration indices occurring in morainic mesophytic forest where growth water is always high; note low transpiration for a day with so low a relative humidity.

3. The foliar transpiring power of *Tilia* was found to increase in dune environments from an index of 0.15 on the forested *Tilia* complex to 0.55 in the most exposed situations on the open sand. In habitats between these extremes the transpiration power was found to be directly proportional to the relative exposure.

4. The morning rise in the daily march is more rapid on the open sand, where it reaches a maximum 1 to 2 hours earlier than in forested situations.

5. In the forested complex the curve representing relative transpiration tends to develop a single mode about midday, and this maximum tends to coincide with the maxima of temperature, relative humidity, and evaporating power of the air. The greater the mesophytism and relative humidity the more striking becomes this tendency.

6. In the most exposed situations on the open sand the relative transpiration maximum usually appears about 10:00 A.M., while the maximum temperature; relative humidity, and evaporating power occur from 2:00 to 4:00 P.M. This divergence from parallelism is due to the development of a saturation deficit, which appears successively earlier as the exposure of the habitat increases. The more mesophytic the habitat the less noticeable becomes this deficit, until it disappears entirely, especially on humid days.

7. The foliar transpiration index is influenced less by wind currents than is the porous cup atmometer.

8. Transpiration curves showing a saturation deficit depression usually develop a second mode about 4:00 P.M., which is, so far as noticed, always lower than the mode preceding the deficit depression.

9. Bimodal transpiration curves have been found to be due either to a saturation deficit or to a sudden increase in relative humidity, although lesser depressions may result from fluctuating temperature or intensity of light.

10. No evidence of visible wilting occurred in *Tilia* on the open sand at any time during the summer, although the so-called "incipient drying" was a common feature of the stations throughout this period. On the forested complex, however, visible wilting occurred during the first week in August because the vegetation was so dense that the water content of the soil was reduced to the wilting coefficient quite early.

11. The average mesophytism on the *Tilia* complex is considerably greater than on the open sand, the growth water averages being 2.5 and 1.25 per cent respectively; but the open positions are practically constant in their water relations, while the forested complex represents a decreasing mesophytism as the summer

advances, the growth water in the spring being higher than at any other time.

12. The amount of growth water in the soil apparently has very little influence on the transpiration index, unless it is reduced to the wilting coefficient. It might be argued that a low growth water is the cause of the saturation deficit depression, but there is evidence that it is due rather to the inability of the translocating system to conduct water to the leaves with sufficient rapidity to offset the transpiration loss, and not to a slowing up of the absorption rate. This is substantiated by the occurrence of the typical deficit in readings on *Tilia* when the growth water was greater than 20 per cent. The drop that occurs when the soil moisture falls to the wilting coefficient is more permanent and is due to stomatal movement which accompanies visible wilting.

I wish to express my grateful appreciation of the encouragement and suggestions given by Dr. Geo. D. Fuller, of the University of Chicago.

College of Emporia
Emporia, Kan.

LITERATURE CITED

1. Bakke, A. L., Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecol. **2**:145–173. 1914.
2. Briggs, L. J., and Shantz, H. L., Daily transpiration during the normal growth period and its correlation with the weather. Jour. Agric. Res. **7**:155–212. 1916.
3. ———, The wilting coefficient and its indirect determination. Bot. Gaz. **53**:20–37. 1912.
4. Briggs, L. J., and McLane, L. W., The moisture equivalent of soils. U.S. Dept. Agric. Bur. Soil Bull. 45. 1907.
5. Fuller, G. D., Evaporation and soil moisture in relation to the succession of plant associations. Bot. Gaz. **58**:193–234. 1914.
6. Livingston, B. E., Light intensity and transpiration. Bot. Gaz. **52**: 417–438. 1911.
7. ———, Atmometry and the porous cup atmometer. Plant World **18**: 21–30, 51–74, 95–111, 143–149. 1915.
8. ———, The resistance offered by leaves to transpirational water loss. Plant World **16**:1–35. 1913.

9. LIVINGSTON, B. E., and BROWN, W. H., Relation of the daily march of transpiration to the variation of the water content of foliage leaves. BOT. GAZ. 53:309–330. 1912.

10. LIVINGSTON, B. E., and SHREVE, EDITH B., Improvements in the methods of determining the transpiring power of plant surfaces by hygrometric paper. Plant World 19:287–309. 1916.

11. LLOYD, F. E., The physiology of stomata. Carnegie Inst. Wash. Publ. no. 82. 1908.

12. MARVIN, C. F., Psychrometric tables for obtaining the vapor pressure, relative humidity, and temperature of the dew point. U.S. Dept. Agric. Weather Bur. Bull. 235. 1912.

13. RENNER, O., Experimentelle Beiträge zur Kenntniss der Wasserbewegung. Flora 103:171–247. 1911.

14. RYSSELBERGHE, F. VAN, Influence de la température sur la permeabilite du protoplasme vivant pour l'eau et les substances dissoutes. Bull. Acad. Belg. 1:173–221. 1901.

15. STAHL, E., Einige Versuche über Transpiration und Assimilation. Bot. Zeit. 52:117–146. 1894.

16. TRELEASE, S. F., and LIVINGSTON, B.E., The daily march of transpiring power as indicated by the porometer and by standardized hygrometric paper. Jour. Ecol. 4:1–14. 1916.